

African Journal of Biotechnology Vol. 5 (25), pp. 2526-2533, 29 December, 2006
Available online at <http://www.academicjournals.org/AJB>
ISSN 1684-5315 © 2006 Academic Journals

Review

Manipulating legume/cereal mixtures to optimize the above and below ground interactions in the traditional African cropping systems

Patrick A. Ndakidemi

Research and Technology Promotion, Cape Peninsula University of Technology, Cape Town Campus,
Keizersgracht, P O Box 652, Cape Town, 8000, South Africa. E-mail: NdakidemiP@cput.ac.za.

Accepted 6 December, 2006

The purpose of mixing legume and cereals in the cropping systems is to optimise the use of spatial, temporal, and physical resources both above- and below ground, by maximising positive interactions (facilitation) and minimising negative ones (competition) among the components. The complex interactions in legume/cereal cropping systems such as those used by traditional farmers have received little research attention. Information from such studies is likely to provide an understanding of plant survival strategies when subjected to stress in mixtures. Current knowledge on how plants in mixtures change their biological and chemical environments and the potential benefits associated with such processes are assessed in this review.

Key words: intercropping, microbial biomass, N₂ fixation, phosphatase activities, pH changes.

INTRODUCTION

Mixed culture (or intercropping) of legumes and cereals is an old practice in tropical agriculture that dates back to ancient civilization. The main objective of intercropping has been to maximise use of resources such as space, light and nutrients (Willey, 1990; Morris and Garrity, 1993; Li et al., 2003b), as well as to improve crop quality and quantity (Nel, 1975; Izaurralde et al., 1990; Mpairwe et al., 2002). Other benefits include water quality control through minimal use of inorganic nitrogen fertilisers that pollute the environment (Crew and Peoples, 2004). The current trend in global agriculture is to search for highly productive, sustainable and environmentally friendly cropping systems (Crew and Peoples, 2004). This has resulted into renewed interest in cropping systems research (Vandermeer, 1989).

When two crops are planted together, interspecific competition or facilitation between plants may occur (Vandermeer, 1989; Zhang et al., 2003). For example,

studies have shown that mixtures of cereals and legumes produce higher grain yields than either crop grown alone (Mead and Willey, 1980; Horwith, 1984; Tariah and Wahua, 1985; Ofori and Stern, 1987a; Lawson and Kang, 1990; Watiki et al., 1993; Peter and Runge-Metzger, 1994; Skovgard and Pats, 1999; Rao and Mathuva, 2000; Olufemi et al., 2001; Mpairwe et al., 2002; Dapaah et al., 2003). In such crop mixtures, the yield increases were not only due to improved nitrogen nutrition of the cereal component, but also to other unknown causes (Nel, 1975; Connolly et al., 2001).

Many of the unknown and less researched processes occur in the rhizosphere of mixtures (Connolly et al., 2001; Zhang et al., 2003, 2004). The rhizosphere soil is the narrow zone of soil surrounding the roots where soil, micro-organisms and roots jointly play key roles in the ecosystem. Compared with the bulk soil, the rhizosphere has different biological, physical and chemical soil properties. It is rich in root exudates, and, therefore, play a major role in nutrient mobilisation and microbial activities (Dakora and Phillips, 2002; Dakora, 2003). So far however, little attention has been paid to rhizosphere effects on crops grown in mixtures (Connolly et al., 2001;

*Corresponding Authors E-mail: muthupriya_03@yahoo.com.
Tel: 04144-239737. Fax: 04144-238275.

Zhang et al., 2003; 2004), where interaction between different organisms is maximal.

The major management practices employed in mixed cultures to attain good yield includes the enhancement of microclimatic conditions, improved utilisation and recycling of soil nutrients, improved soil quality, provision of favourable habitats for plants and stabilisation of soil, among others (Juma et al., 1997). These conditions are achieved by manipulating management practices such as planting patterns of the mixtures.

Although monoculture systems involving cereals and legumes are well researched many of the complex mixed systems such as those practised by farmers in Africa have received little attention. For example, many planting patterns for legumes and cereals exist in Africa whose belowground interactions have received little research attention and hence their ecology still explored (Connolly et al., 2001).

Intercropping systems are deliberately designed and manipulated to optimise the use of spatial, temporal, and physical resources both above- and belowground, by maximising positive interactions (facilitation) and minimising negative ones (competition) among the components (Willey and Osiru, 1972; Willey, 1979; Mead and Willey, 1980; Horwith, 1985; Ofori and Stern, 1986, 1987a, b; Jose et al., 2000; Silwana and Lucas, 2002). An understanding of the biological and chemical processes and mechanisms involved in the allocation of resources in such systems is essential. The complex interactions in legume/cereal cropping systems such as those used by traditional farmers have received little research attention (Connolly et al., 2001; Zhang et al., 2004) because quantitative rhizosphere studies in the field involving complex mixtures are notoriously difficult and cumbersome. Information from such studies is likely to provide an understanding of plant survival strategies when subjected to stress in mixtures.

INTERACTIONS BETWEEN PLANTS IN MIXTURES

Plant-to-plant interactions can occur in the above- or below-ground plant compartments. Interactions will occur in the growth process, especially when the component species are exploiting growth resources above-and below-ground (Vandermer, 1989; Willey, 1990; Ong et al., 1996) from the same location or at the same time. In crop mixtures, any species utilizing the same combination of resources will be in direct competition. However, based on differences in phenological characteristics of species in mixtures, the interaction among them may lead to an increased capture of a limiting growth resource (Willey and Osiru, 1972; Willey, 1979; Mead and Willey, 1980; Horwith, 1985; Ofori and Stern, 1986, 1987a,b; Silwana and Lucas, 2002) and then accrue greater total yield than the cumulative production of those species if they were grown separately on an equivalent land area (Mead and

Willey, 1980; Horwith, 1984; Tariah and Wahua, 1985; Ofori and Stern, 1987a; Lawson and Kang, 1990; Watiki et al., 1993; Peter and Runge-Metzger, 1994; Myaka, 1995; Asafu-Agyei et al., 1997; Skovgard and Pats, 1999; Rao and Mathuva, 2000; Olufemi et al., 2001; Dapaah et al., 2003). Thus, mixed culture systems between cereals and legumes may experience a complex series of inter- and intra-specific interaction (Izaurrealde et al., 1990; Giller and Cadisch, 1995; Evans et al., 2001; Li et al., 2003c) guided by modifications and utilisation of light, water, nutrients and enzymes. More studies are needed to quantify such interactions in different legume/cereal mixtures such as those used by farmers in Africa.

Rhizosphere interaction in legume cereal mixtures

Most annual crop mixtures such as those involving cereals and legumes are grown almost at the same period, and develop root systems that explore the same soil zone for resources (Horwith, 1984; Chang and Shibles, 1985a,b; Reddy et al., 1994; Jensen et al., 2003). Under such conditions, below-ground competition for resources such as nutrients is most likely to occur. For example, research has shown that activities in mixed cropping systems involving maize and cowpea occur between the top 30 – 45 cm of soil, and their density decreased with depth (Maurya and Lal, 1981; McIntyre et al., 1997). Because of these interactions, cowpea yields can be reduced significantly relative to that of maize (Watiki et al., 1993). In contrast to some negative effects on yield, root systems in mixtures may provide some of the major favorable effects on soil and plants. These include, amongst others, carbon enrichment through carbon turnover (Ridder et al., 1990; Vanlauwe et al., 1997), release of phenolics, phytosiderophores and carboxylic acids as root exudates by component plants (Dakora and Phillips, 2002; Dakora, 2003). These molecules play a major role in the mineral nutrition of plants. For instance, some studies have shown that, in P-deficient soils, pigeon pea roots use piscidic, malonic, and oxalic acids to solubilise Fe-, Ca- and Al-bound P (Ae et al., 1990). Once mobilised, P and Fe then become available for uptake by the pigeon pea plant as well as by other associated plant species and micro flora in the cropping system.

In aluminum-toxic soils, oxalate released by buckwheat roots forms an Al-oxalate complex that renders the Al non-toxic to plants and mutualistic microbes in the cropping system (Ma et al., 1998). In that way, productivity of the cultural system is enhanced. Whether similar processes take place in legume-cereal mixtures such as those used in Africa, and the extent to which they affect the below ground activities, need to be established. This is due to the fact that, thus far, research efforts on mixed cultures has centered on the intra- and inter-specific competition for light and water, and research reports on competition for nutrients in legumes and cereal mixtures

in Africa are limited (Connolly et al., 2001; Zhang et al., 2003, 2004). It is, therefore, of greater importance to explore how the rhizosphere systems of the associated plant species in mixtures interact under different legume-cereal cropping systems.

Rhizospheric pH changes in different management systems in legume/cereal mixtures

Many plants have the ability to modify the pH of their rhizosphere (Hoffland et al., 1989, 1992; Raven et al., 1990; Degenhardt et al., 1998; Muofhe and Dakora, 2000; Dakora and Phillips, 2002) and enhance nutrient availability such as P, K, Ca, and Mg, which are otherwise fixed in unavailable forms (Vandermeer, 1989; Hagggaard-Nielson and Jensen, 2005). For instance, legumes induce several reactions that modify the rhizosphere pH (Jarvis and Robson, 1983; McLay et al., 1997; Tang et al., 1998, 2001) and affect nutrient uptake (Brady, 1990; Vizzatto et al., 1999). For example, Dakora et al. (2000) have shown that due to pH changes in the rhizosphere, *Cyclopia genistoides*, a tea-producing legume indigenous to South Africa, increased nutrient availability in its rhizosphere by 45 – 120% for P, 108 – 161% for K, 120 – 148% for Ca, 127 – 225% for Mg and 117 – 250% for boron (B) compared with bulk non-rhizosphere soil. Hence, legumes may take up higher amounts of base cations, and in the process of balancing internal charge, release H⁺ ions into the rhizosphere that results in soil acidification (Jarvis and Robson, 1983; McLay et al., 1997; Tang et al., 1998, 2001; Sas et al., 2001; Dakora and Phillips, 2002; Cheng et al., 2004). Other legumes such as alfalfa, chickpea, lupines, and cowpea can release considerable amounts of organic anions and lower their rhizosphere pH (Liptone et al., 1987; Dinkelaker et al., 1989, 1995; Braum and Helmke, 1995; Gilbert et al., 1999; Neumann et al., 1999; Rao et al., 2002; Li et al., 2004b), a condition conducive for the hydrolysis of organic P and hence improving P nutrition for plants and micro organism in the soil. In the same context, white lupine (*Lupinus albus*) exuded organic acids anions and protons that lowered rhizosphere pH and recovered considerable amounts of P from the soil and made them more available to wheat than when it was grown in a monoculture (Horst and Waschkies, 1987; Kamh et al., 1999). Similarly, pigeon pea increased P uptake of the intercropped sorghum by exuding piscidic acid anions that chelated Fe³⁺ and subsequently released P from FePO₄ (Ae et al., 1990). In a field experiment, faba bean facilitated P uptake by maize (Zhang et al., 2001; Li et al., 1999, 2003b; Zhang and Li, 2003). In another comparative study, the ability of chickpea to mobilise organic P was shown to be greater than that of maize due to greater exudation of protons and organic acids by chickpea relative to maize (Li et al., 2004a).

Thus, in mixed cultures, plants such as cereals, which do not have strong rhizosphere acidification capacity can benefit directly from nutrients solubilised by legume root exudates. What is, however, not clearly known is the extent of rhizosphere pH changes in mixed cultures involving nodulated legumes and cereals and their influence on other biological and chemical processes in the soil.

N₂ FIXATION IN LEGUMES AND THE ASSOCIATED BENEFITS TO THE CEREAL COMPONENT

Biological nitrogen fixation by grain legume crops has received a lot of attention (Eaglesham et al., 1981; Giller et al., 1991; Izaurralde et al., 1992; Giller and Cadisch, 1995; Peoples et al., 2002) because it is a significant N source in agricultural ecosystems (Heichel, 1987; Dakora and Keya, 1997). However, studies on N₂ fixation in complex cereal/legume mixtures are few (Stern, 1993; Peoples et al., 2002). Intercropping usually includes a legume which fixes N₂ that benefits the system, and a cereal component that depends heavily on nitrogen for maximum yield (Ofori and Stern, 1986; Cochran and Schlentner, 1995). Controlled studies have shown a significant direct transfer of fixed-N to the associated non-legume species (Eaglesham et al., 1981; Giller et al., 1991; Frey and Schüepp, 1993; Stern, 1993; Elgersma et al., 2000; Høgh-Jensen and Schjoerring, 2000; Chu et al., 2004). There is evidence that the mineralisation of decomposing legume roots in the soil can increase N availability to the associated crop (Dubach and Russelle, 1994; Schroth et al., 1995; Evans et al., 2001). In mixed cultures, where row arrangements and the distance of the legume from the cereal are far, nitrogen transfer could decrease. Research has shown that competition between cereals and legumes for nitrogen may in turn stimulate N₂ fixation activity in the legumes (Fujita et al., 1990; Hardarson and Atkins, 2003). The cereal component effectively drains the soil of N, forcing the legume to fix more N₂. Therefore it is important to manipulate and establish how the management practice in legume/cereal mixtures may influence N₂ fixation and nutrition in the traditional African cropping systems.

SOIL MICROBIAL BIOMASS IN LEGUME/CEREAL MIXTURES

The microbial biomass is influenced by biological, chemical, and physical properties of the plant-soil system. Generally, soil and plant management practices may have greater influence on the level of soil microbial C (Gupta and Germida, 1988; Dick et al., 1994; Dick, 1997; Alvey et al., 2003). For instance, soil microbial C tend to show the highest values in cropland and grassland soils and the lowest in bare cultivated soils (Brookes et al., 1984; Gupta and Germida, 1988).

Monoculture systems are expected to contain reduced amounts of microbial biomass and activities in compari-

son to those in mixed cultures (Moore et al., 2000). Studies have indicated that legumes accumulated greater amounts of soil microbial C in the soil than cereals (Walker et al., 2003). This is attributed to lower C:N ratio of legume than that of cereal (Uriyo et al., 1979; Brady, 1990).

Microbial biomass activities could increase after the addition of an energy source. The stimulation of soil microbial biomass activity by organic amendments is higher than that induced by organic fertilisers (Bolton et al., 1985; Goyal et al., 1993; Höflich et al., 2000). Soil organic matter content and soil microbial activities, vital for the nutrient turnover and long term productivity of soil, are enhanced by the balanced application of nutrient and/or organic matter/manure (Bolton et al., 1985; Guan, 1989; Goyal et al., 1993; Höflich et al., 2000; Kanchikerimath and Singh, 2001). Under conditions of adequate nutrient supply such as P, the microbial biomass C will be increased due to improved plant growth and increased turnover of organic matter in the soil (Bolton et al., 1985). Whether the management practices in mixed cultures involving legumes and cereals may favour the stimulation of biological soil activity and, thus, result in a higher turnover of organic substrates in the soil that are utilised by micro-organisms is a good subject to be investigated.

Although there is a lot of information that show the relationship between soil management and soil microbial activity, little is known about these effects under mixed cultures such as those practised by farmers in the tropical / subtropical environments (Dick, 1984; Dick et al., 1988; Deng and Tabatabai, 1996). In this context, the measurement of their activities could provide useful information concerning soil health, and also serve as a good index of biological status in different crop management systems.

PHOSPHATASE ACTIVITY IN LEGUME/CEREAL MIXTURES

Plants have evolved many morphological and enzymatic adaptations to tolerate low phosphate availability. This includes transcription activity of acid phosphatases, which tends to increase under P starvation (Tarafdar and Jungk, 1987; Goldstein, 1992; Duff et al., 1994; del Pozo et al., 1999; Haran et al., 2000; Baldwin et al., 2001; Miller et al., 2001; Li et al., 2002). Phosphatase enzymes in the soil serve several important functions, and are good indicators of soil fertility (Dick and Tabatabai, 1992; Eivazi and Tabatabai, 1997; Dick et al., 2000). Under conditions of P deficiency, acid phosphatase secreted from roots is increased (Nakas et al., 1987; Chrost, 1991; Hayes et al., 1999; Li et al., 1997). Gilbert et al. (1999) found that white lupin roots from P-deficient plants had significantly greater acid phosphatase activity in both the root extracts and the root exudates than comparable samples from P-sufficient plants. At different stress levels, these enzymes release phosphate from both cellular (Bariola et al., 1994) and extra cellular (Duff et al.,

1994) organic compounds. The transcripts and activity of phosphate transporters are increased to optimise uptake and remobilisation of phosphate in P-deficient plants (Muchhal et al., 1996; Daram et al., 1999; Kai et al., 2002; Karthikeyan et al., 2002; Mudge et al., 2002; Versaw and Harrison, 2002). It is thought that these morphological and enzymatic responses to P starvation are coordinated by both general stress-related and P-specific signalling systems.

The amount of acid phosphatase secreted by plants is genetically controlled, and differs with crop species and varieties (Izaguirre-Mayoral and Carballo, 2002) as well as crop management practices (Patra et al., 1990; Staddon et al., 1998; Wright and Reddy, 2001). Some studies have shown that the amount of enzymes secreted by legumes were 72 % higher than those from cereals (Yadav and Tarafdar, 2001). Li et al. (2004a) found that, chickpea roots were also able to secrete greater amounts of acid phosphatase than maize. The activity of acid phosphatases is expected to be higher in biologically managed systems because of higher quantity of organic C found in those systems. In fact, the activity of acid and alkaline phosphatase was found to correlate with organic matter in various studies (Guan, 1989; Jordan and Kremer, 1994; Aon and Colaneri, 2001).

It is, therefore, anticipated that management practices in mixed cultures that induce P stress in the rhizosphere, may also affect the secretion of these enzymes. To date, there have been few studies examining the influence of cropping system on the phosphatase activity in the rhizosphere of most legumes and cereals grown in Africa. Understanding the dynamics of enzyme activities in these systems is crucial for predicting their interactions as in turn their activities may regulate nutrient uptake and plant growth in the ecosystem.

CONCLUSION

Future research should focus on manipulating the legume /cereal mixtures and establish different survival mechanisms that are used by the plants in stressed environments. Efforts should be geared towards closing the existing gap in rhizosphere research in mixed cultures by correctly outlining the unknown factors that affects plant growth in mixtures. This can lead to increased production through improved plant nutrition, as well as genetic manipulation of different plant species and management practices in the cropping systems.

ACKNOWLEDGEMENT

This study was supported with a competitive grant awarded by the Department of Science and Technology, Pretoria, under the auspices of the SADC Science and Technology Research Fund as well as financial support from the Cape Peninsula University of Technology.

REFERENCES

- Ae N, Arihara J, Okada K (1990). Phosphorus uptake by pigeon pea and its role in cropping systems of the Ind. subcontinent. *Sci.* 248: 477-480.
- Alvey S, Yang CH, Buerkert D, Crowley DE. (2003). Cereal/legume rotation effects on rhizosphere bacterial community structure in West African soils. *Biol. Fertility of Soils* 37: 73-82.
- Aon MA, Colaneri AC. (2001). Temporal and spatial evolution of enzymatic activities and physico-chemical properties in an agricultural soil. *Appl. Soil Ecol.* 18: 255-270.
- Asafu-Agyei JN, Ahenkora K, Banful B, Ennin-Kwabiah S. (1997). Sustaining food production in Ghana: In 'The role of cereal-legume based cropping systems'. In: Bezunch T, Emechebe AM, Sedago J, Quedraogo M. (eds.) Semi-Arid Food Grain Research and Development Agency of the Scientific, Technical and Research Commission of OAU, Quagadougou, Burkina Faso. pp. 409-416.
- Baldwin JC, Karthikeyan AS, Raghothama KG. (2001). *LEPS2*, a phosphorus starvation-induced novel acid phosphatase from tomato. *Plant Physiol.* 125: 728-737.
- Bariola PA, Howard CJ, Taylor CB, Verburg MT, Jaglan VD, Green PJ (1994). The *Arabidopsis* ribonuclease gene *RNS1* is tightly controlled in response to phosphate limitation. *Plant J.* 6: 673-685.
- Bolton H, Elliot LF, Papendick RI, Bezdicsek DF. (1985). Soil microbial biomass and selected soil enzyme activities: effect of fertilization and cropping practices. *Soil Biol. Biochem.* 17: 297-302.
- Brady N (1990). The Nature and Properties of Soils, Tenth Edition. Macmillan Publ. Co., New York, 621 pp.
- Braum SM, Helmke PA (1995). White lupin utilizes soil phosphorus that is unavailable to soybean. *Plant and Soil* 176: 95-100.
- Brookes PC, Powlson DS, Jenkinson DS (1984). Phosphorus in the soil microbial biomass. *Soil Biol. Biochem.* 16:169-175.
- Chang JF, Shibles RM (1985a). An analysis of competition between intercropped cowpea and maize I. Soil N and P levels and their relationships with dry matter and seed productivity. *Field Crops Res.* 12: 133-143.
- Chang JF, Shibles RM (1985b). An analysis of competition between intercropped cowpea and maize II. The effect of fertilization and population density. *Field Crops Res.* 12: 145-152.
- Cheng Y, Howieson JG, O'Hara GW, Watkin ELJ, Souche G, Jaillard B, Hinsinger P (2004). Proton release by roots of *Medicago murex* and *Medicago sativa* growing in acidic conditions, and implication for rhizosphere pH changes and nodulation at low pH. *Soil Biol. Biochem.* 36: 1357-1365.
- Chrost R (1991). Environmental control of the synthesis and activity of aquatic microbial ectoenzymes. In: Chrost RJ (ed.) Microbial enzymes in aquatic environments. Springer-Verlag, New York pp 29-59.
- Chu GX, Shen QR, Cao JL (2004). Nitrogen fixation and transfer from peanut to rice cultivated in aerobic soil in an intercropping system and its effect on soil N fertility. *Plant and Soil* 263: 17-27.
- Cochran VL, Schlentner SF (1995). Intercropped oat and faba bean in Alaska: Dry matter production, dinitrogen fixation, nitrogen transfer, and nitrogen fertilizer response. *Agronomy J.* 87: 420-424.
- Connolly J, Goma HC, Rahim K (2001). The information content of indicators in intercropping research. *Agric. Ecosyst. Environ.* 87: 191-207.
- Crew TE, Peoples MB (2004). Legume versus fertilizer source of nitrogen: ecological tradeoffs and human needs. *Agric. Ecosyst. Environ.* 102: 279-297.
- Dakora FD, Keya SO (1997). Contribution of legume nitrogen fixation to sustainable agriculture in Sub-Saharan Africa. *Soil Biol. Biochem.* 29: 809-817.
- Dakora FD, Phillips D (2002). Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant and Soil* 245: 35-47.
- Dakora FD, Spriggs A, Nyemba RC, Chimphango SMB (2000). Host-plant factors in the adaptation of indigenous African legumes to low pH soils. In: Pedrosa FO, Hungria M, Yates MG, Newton WE. (eds.) Nitrogen Fixation from molecules to Crop Productivity. Dordrecht, the Netherlands: Kluwer Academic Publishers, 579-580.
- Dakora FD (2003). Defining new roles for plant and rhizobial molecules in sole and mixed plant cultures involving symbiotic legumes. *New Phytol.* 158: 39-49.
- Dapaah HK, Asafu-Agyei JN, Ennin SA, Yamoah C (2003). Yield stability of cassava, maize, soya bean and cowpea intercrops. *J. Agric. Sci.* 140: 73-82.
- Daram P, Brunner S, Rausch C, Steiner C, Amrhein N, Bucher M (1999). *Pht2;1* encodes a low affinity phosphate transporter from *Arabidopsis*. *Plant Cell* 11: 2153-2166.
- Degenhardt J, Larsen PB, Howell SH, Kochian LV (1998). Aluminium resistance in the *Arabidopsis* mutant *alr-104* is caused by an aluminium-induced increase in pH. *Plant Physiol.* 117: 19-27.
- del Pozo JC, Allona I, Rubio V, Leyva A, de la Peña A, Aragoncillo C, Paz-Ares J (1999). A type 5 acid phosphatase gene from *Arabidopsis thaliana* is induced by phosphate starvation and by some other types of phosphate mobilising/oxidative stress conditions. *Plant J.* 19: 579-589.
- Deng SP, Tabatabai MA (1996). Effect of tillage and residue management on enzyme activities in soils: II. Glycosidases. *Biol. Fertility of Soils* 22: 208-213.
- Dick WA, Tabatai MA. (1992). Significance and potential uses of soil enzymes. In: Metting Jr., FB (ed.) Soil Microbial Ecology, Marcel Dekker, New York, NY USA, pp. 95-127.
- Dick WA, Cheng L, Wang P (2000). Soil acid and alkaline phosphatase activity as pH adjustment indicators. *Soil Biol. Biochem.* 32: 1915-1919.
- Dick RP (1997). Soil enzyme activities as integrative indicators of soil health. In: Pankhurst, CE, Doube BM, Gupta VVSR. (eds.) Biological Indicators of Soil Health. CAB International, p.121-156.
- Dick RP, Rasmussen PE, Kerle EA (1988). Influence of long-term residue management on soil enzyme activities in relation to soil chemical properties of a wheat-fallow system. *Biol. Fertility of Soils* 6: 159-164.
- Dick RP, Sandor JA, Eash NS (1994). Soil enzyme activities after 1500 years of terrace agriculture in the Colca Valley, Peru. *Agric. Ecosyst. Environ.* 50: 123-131.
- Dick WA (1984). Influence of long-term tillage and crop rotation combinations on soil enzyme activities. *Soil Sci. Soc. Am. J.* 48: 569-574.
- Dinkelaker B, Hengeler C, Marschner H (1995). Distribution and function of proteoid roots and other root clusters. *Botanica Acta* 108: 183-200.
- Dinkelaker B, Römhild V, Marschner H (1989). Citric acid excretion and precipitation of calcium citrate in the rhizosphere of white lupin (*Lupinus albus* L.) *Plant Cell and Environ.* 12: 285-292.
- Dubach M, Russelle MP (1994). Forage legume roots and nodules and their role in nitrogen transfer. *Agron. J.* 86: 259-266.
- Duff SMG, Sarath G, Plaxton WC (1994). The role of acid phosphatases in plant phosphorus metabolism. *Physiol. Plantarum* 90: 791-800.
- Eaglesham ARJ, Ayanaba A, Ranga Rao V, Eskew DL (1981). Improving the nitrogen nutrition of maize by intercropping with cowpea. *Soil Biol. Biochem.* 13: 169-171.
- Eivazi, F, Tabatai MA (1997). Phosphatase in soils. *Soil Biol. Biochem.* 9: 167-172.
- Elgersma A, Schlegers H, Nassiri M (2000). Interactions between perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) under contrasting nitrogen availability: productivity, seasonal patterns of species composition, N₂ fixation, N transfer and N recovery. *Plant and Soil* 221: 281-299.
- Evans J, McNeill AM, Unkovich MJ, Fettel NA, Heenan DP (2001). Net nitrogen balances for cool-season grain legume crops and contributions to wheat nitrogen uptake: a review. *Austr. J. Exp. Agric.* 41: 347-359.
- Frey B, Schüepp H (1993). A role of vesicular-arbuscular (VA) mycorrhizal fungi in facilitating interplant nitrogen transfer. *Soil Biol. Biochem.* 25: 651-658.
- Fujita K, Ogata S, Matsumoto K, Masuda T, Godfred K, Ofosu-Budu KG, Kuwata K (1990). Nitrogen transfer and dry matter production in soybean and sorghum mixed cropping system at different population densities. *Soil Sci. Plant Nutrition* 36: 233-241.
- Gilbert GA, Knight JD, Vance CP, Allan DL (1999). Acid phosphatase activity in phosphorus-deficient white lupin roots. *Plant, Cell and Environ.* 22: 801-810.
- Giller KE, Ormsher J, Awah F (1991). Nitrogen transfer from Phaseolus

- bean to intercropped maize measured using ^{15}N -enrichment and ^{15}N -isotope dilution methods. In: Dommergues YR, Krupa SV. (eds.) *Soil Microorganisms and Plants*. Elsevier, Amsterdam pp 163-203.
- Giller KE, Cadisch G (1995). Future benefits from biological nitrogen fixation: an ecological approach to agriculture. *Plant and Soil* 174: 255-277.
- Goldstein AH (1992). Phosphate starvation inducible enzymes and proteins in higher plants. In: JL Wray JL. (ed.) *Society for Experimental Biology Seminar Series 49: Inducible Plant Proteins*. Cambridge University Press, Cambridge, pp 25-44.
- Goyal S, Mishra MM, Dhankar SS, Kapoor KK, Batra R (1993). Microbial biomass turnover and enzyme activities following application of farm yard manure to field soils with and without previous long-term application. *Biol. Fertility of Soils* 15: 60-64.
- Guan SY (1989). Studies on the factors influencing soil enzyme activities: I. Effects of organic manures on soil enzyme activities and N and P transformations. *Acta Pedol. Sinica* 26: 72 - 78.
- Gupta VVSR, Germida JJ (1988). Distribution of microbial biomass and its activity in different soil aggregate size classes as affected by cultivation. *Soil Biol. Biochem.* 20: 777-786.
- Haran S, Logendra S, Sesar M, Bratanova M, Raskin I (2000). Characterization of *Arabidopsis* acid phosphatase promoter and regulation of acid phosphatase expression. *Plant Physiol.* 124: 615-626.
- Hardason G, Atkins G (2003). Optimizing biological N_2 fixation by legumes in farming systems. *Plant and Soil.* 252: 41-54.
- Hauggaard-Nielsen H, Jensen ES (2005). Facilitative root interactions in intercrops. *Plant and Soil* 274: 237-250.
- Hayes JE, Richardson AE, Simpson RJ (1999). Phytase and acid phosphatase activities and extracts from roots of temperate pasture grass and legume seedlings. *Austr. J. Plant Physiol.* 26: 801-809.
- Heichel GH (1987). Legume nitrogen: Symbiotic fixation and recovery by subsequent crops. In: Helsel ZR. (ed.) *Energy in Plant Nutrition and Pest Control*. Elsevier Sci. Publ.. Amsterdam pp 63-80.
- Hoffland E, van den Boogaard R, Nelemans JA, Findenegg GR (1992). Biosynthesis and root exudation of citric and malic acid in phosphate starved rape plants. *New Phytol.* 122: 675-680.
- Hoffland E, Findenegg GR, Nelemans JA (1989). Solubilization of rock phosphate by rape. II. Local root exudation of organic acids as a response to P-starvation. *Plant and Soil* 113: 161-165.
- Höflich G, Tauschke M, Kühn G, Rogasik J (2000). Influence of agricultural crops and fertilization on microbial activity and microorganisms in the rhizosphere. *J. Agron. Crop Sci.* 184: 49-54.
- Hogh-Jensen H, Schjoerring JK (2000). Below-ground nitrogen transfer between different grassland species: Direct quantification by ^{15}N . *Plant and Soil* 227: 171-183.
- Horst BG, Waschkies C (1987). Phosphorus nutrition of spring wheat in mixed culture with white lupin (*Lupinus albus* L.). *Zeitschrift für Pflanzenernährung und Bodenkunde* 150: 1-8.
- Horwith B (1984). A role for intercropping in modern agriculture. *BioSci.* 35: 286-291.
- Izaguirre-Mayoral ML, Flores S, Carballo O (2002). Determination of acid phosphatase and dehydrogenase activities in the rhizosphere of nodulated legume species native to two contrasting savannas in Venezuela. *Biol. Fertility of Soils* 35: 470-472.
- Izaurrealde RC, Juma NG, McGill WB (1990). Crop and nitrogen yield of barley and barley-field pea intercrop in cryoboreal-subhumid central Alberta. *Agron. J.* 82: 295-301.
- Izaurrealde RC, McGill WB, Juma NG (1992). Nitrogen fixation efficiency, interspecies N transfer, and root growth in barley-field pea intercrop on a Black Chernozemic soil. *Biol. Fertility of Soils* 13: 11-16.
- Jarvis SC, Robson AD (1983). The effect of nitrogen nutrition of plants on the development of acidity in western Australian soils. Effects with subterranean clover grown under leaching conditions. *Austr. J. Agric. Res.* 34: 341-353.
- Jensen JR, Bernhard RH, Hansen S, McDonagh J, Moberg JP, Nielsen NE, Nordbo E (2003). Productivity in maize based cropping systems under various soil-water-nutrient management strategies in a semi-arid, alfisol environment in East Africa. *Agric. Water Management* 59: 217-237.
- Jordan D, Kremer RJ (1994). Potential use of soil microbial activity as an indicator of soil quality. In: Pankhurst CE, Doube BM, Gupta VVSR, Grace PR. (eds.): *Soil biota: management in sustainable farming systems*, CSIRO Australia. pp 245-249.
- Jose S, Gillespie AR, Seifert JR, Mengel DB, Pope PE (2000). Defining competition vectors in temperate alley cropping system in the mid-western USA. 3. Competition for nitrogen and litter decomposition dynamics. *Agroforestry Systems* 48: 61-77.
- Juma NG, Izaurrealde RC, Robertson JA, McGill WB (1997). Crop yield and soil organic matter trends over 60 years in a Typic Cryoboralf at Breton, Alberta. In: Paul, EA, Paustian K, Elliott ET, Cole CV. (eds.) *Soil Organic Matter in Temperate Agroecosystems. Long-term Experiments in North America*. CRC Press, Boca Raton. pp 273-281.
- Kai M, Takazumi K, Adachi H, Wasaki J, Shinano T, Osaki M (2002). Cloning and characterisation of four phosphate transporter cDNAs in tobacco. *Plant Sci.* 163: 837-846.
- Kamh M, Horst WJ, Amer F, Mostafa H, Maier P (1999). Mobilization of soil and fertilizer phosphate by cover crops. *Plant and Soil* 211: 19-27.
- Kanchikerimath M, Singh D (2001). Soil organic matter and biological properties after 26 years of maize – wheat – cowpea cropping as affected by manure and fertilization in a Cambisol in semiarid region of India. *Agric. Ecosyst. Environ.* 86: 155-162.
- Karthikeyan AS, Varadarajan DK, Mukatira UT, Panio D'Urzo M, Damsz B, Raghothama KG (2002). Regulated expression of Arabidopsis transporters. *Plant Physiol.* 130: 221-233.
- Lawson TL, Kang BT (1990). Yield of maize and cowpea in an alley cropping system in relation to available light. *Agric. Forest Meteorol.* 52: 347-350.
- Li D, Zhu H, Liu K, Liu X, Leggewie G, Udvardi M, Wang D (2002). Purple acid phosphatases of *Arabidopsis thaliana*. *J Biol Chem* 277: 27772-27781.
- Li L, Tang C, Rengel Z, Zhang FS (2004b). Calcium, magnesium and microelement uptake as affected by phosphorus sources and interspecific root interactions between wheat and chickpea. *Plant and Soil* 261: 29-37.
- Li L, Zhang FS, Li XL, Christie P, Sun JH, Yang SC, Tang C (2003b). Interspecific facilitation of nutrient uptake by intercropped maize and faba bean. *Nutrient Cycling in Agroecosystems* 68: 61-71.
- Li L, Tang C, Rengel Z, Zhang FS (2003a). Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source. *Plant and Soil* 248: 297-303.
- Li MG, Osaki M, Rao IM, Tadano T. 1997. Secretion of phytase from the roots of several plant species under phosphorus conditions. *Plant and Soil* 195: 161-169.
- Li L, Yang SC, Li XL, Zhang FS, Christie P (1999). Interspecific complementary and competitive interactions between intercropped maize and faba bean. *Plant and Soil.* 212: 105-114.
- Li SM, Li L, Zhang FS, Tang C (2004a). Acid Phosphatase Role in Chickpea/Maize Intercropping. *Annals of Botany* 94: 297-303.
- Li WX, Li L, Sun JH, Zhang FS, Christie P (2003c). Effects of nitrogen and phosphorus fertilizers and intercropping on uptake of nitrogen and phosphorus by wheat, maize and faba bean. *J. Plant Nutrition* 26: 629-642.
- Liptone DS, Blanchar RW, Blevins DG (1987). Citrate, malate and succinate concentration in exudates of from P-sufficient and P-stressed *Medicago sativa* L. seedlings. *Plant Physiology* 85: 315-317.
- Ma JF, Hiradate S, Matsumoto H (1998). High aluminium resistance in buckwheat. II Oxalic acid detoxifies aluminium internally. *Plant Physiol.* 117: 753-759.
- Maurya PR, Lal R (1981). Effects of different mulch materials on soil properties and on the root growth and yield of maize (*Zea mays*) and cowpea (*Vigna unguiculata*). *Field Crops Res.* 33: 45-53.
- McLay CDA, Barton L, Tang C (1997). Acidification potential of ten grain legume species grown in nutrient solution. *Austr. J. Agric. Res.* 48: 1025-1032.
- McIntyre BD, Riha SJ, Ong CK (1997). Competition for water in a hedge-intercrop system. *Field Crops Res.* 52: 151-160.
- Mead R, Willey RW (1980). The concept of a 'Land Equivalent Ratio' and advantages in yields from intercropping. *Exp. Agric.* 16: 217-228.
- Miller SS, Liu J, Allan DL, Menzhuber CJ, Fedorova M, Vance CP (2001). Molecular control of acid phosphatase secretion into the rhizosphere of proteoid roots from phosphorus-stressed white lupin. *Plant Physiol.* 127: 594-606.

- Moore JM, Klose S, Tabatai MA. (2000). Soil microbial biomass carbon and nitrogen as affected by cropping systems. *Biol. Fertility of Soils* 31: 200-210.
- Morris RA, Garrity DP (1993). Resource capture and utilization in intercropping: non-nitrogen nutrients. *Field Crops Res.* 34: 319-334.
- Mpairwe DR, Sabiiti EN, Ummuna NN, Tegegne A, Osuji P (2002). Effect of intercropping cereal crops with forage legumes and source of nutrients on cereal grain yield and fodder dry matter yields. *Afr. Crop Sci. J.* 10: 81-97.
- Muchhal US, Pardo JM, Raghothama KG (1996). Phosphate transporters from the higher plant *Arabidopsis thaliana*. *Proceedings of National Academy of Science USA* 93: 10519-10523.
- Mudge SR, Rae AL, Diatloff E, Smith FW (2002). Expression analysis suggests novel roles for members of Pht1 family of phosphate transporters in *Arabidopsis*. *Plant J.* 31: 341-353.
- Muofhe ML, Dakora FD (2000). Modification of rhizosphere pH by the symbiotic legume *Aspalathus linearis* growing in a sandy acidic soil. *Austr. J. Plant Physiol.* 27: 1169-1173.
- Myaka FA (1995). Effect of time of planting and planting pattern of different cowpea cultivars on yield of intercropped cowpea and maize in tropical sub-humid environment *Tropical Sci.* 35, 274-279.
- Nakas JP, Gould WD, Klein DA (1987). Origin and expression of phosphatase activity in a semi-arid grassland soil. *Soil Biol. Biochem.* 19: 13-18.
- Nel PC (1975). Mixed cropping of lupines and winter cereals. 4. Seeds yield and quality under field conditions. *J. Agric. Sci.* 8: 219-237.
- Neumann G, Massonneau A, Martinoia E, Römhelt V (1999). Physiological adaptations to phosphorus deficiency during proteoid root development in white lupin. *Planta* 208: 373-382.
- Ofori F, Stern WR (1987a). Cereal-Legume intercropping systems. *Advances in Agron.* 41: 41-90.
- Ofori F, Stern WR (1987b). The combined effects of nitrogen fertilizer and density of the legume component on production efficiency in a maize/cowpea intercrop system. *Field Crops Res.* 16: 43-52.
- Ofori F, Stern WR (1986). Maize/cowpea intercrop system: Effect of nitrogen fertilizer on productivity and efficiency. *Field Crops Res.* 14: 247-261.
- Olufemi O, Pitan R, Odebiyi JA (2001). The effect of intercropping with maize on the level of infestation and damage by pod-sucking bugs in cowpea. *Crop Protection* 20: 367-372.
- Ong CK, Black CR, Marshal FM, Corlet JE (1996). Principles of resource capture and utilization of light and water. In: Ong CK and Huxley P (eds.), *Tree-Crop Interactions: A Physiological Approach*. CAB International, Wallingford, UK pp73-158.
- Patra DD, Brookes PC, Coleman K, Jenkinson DS (1990). Seasonal changes of soil microbial biomass in an arable and a grassland soil which have been under uniform management for many years. *Soil Biol. Biochem.* 8: 249-253.
- Peoples MB, Giller KE, Herridge DF, Vessey JK (2002). Limitations to biological nitrogen fixation as a renewable source for nitrogen for agriculture. In: Finan T, O'Brien M, Layzell D, Vessey K, Newton W. (eds.), *Nitrogen Fixation: Global Perspective*. CAB International, UK pp356-360.
- Peter G, Runge-Metzger A (1994). Monocropping, intercropping or crop rotation? An economic case study from the West African Guinea savannah with special reference to risk. *Agric. Syst.* 45: 123-143.
- Rao MR, Mathuva MN (2000). Legumes for improving maize yields and income in semi-arid Kenya. *Agric. Ecosyst. Environ.* 78: 123-137.
- Rao TP, Yano K, Iijima M, Yamauchi A, Tatsumi J (2002). Regulation of rhizosphere by photosynthetic activity in cowpea (*Vigna unguiculata* L. Walp) seedlings. *Annals of Bot.* 89: 213-220.
- Raven JA, Franco AA, de Jesus EL, Jacob-Neto J (1990). H⁺ extrusion and organic-acid synthesis in N₂-fixing symbioses involving vascular plants. *New Phytol.* 114: 369-389.
- Reddy KC, Visser PL, Klaij MC, Renard C (1994). The effects of sole and traditional intercropping of millet and cowpea on soil and crop productivity. *Exp. Agric.* 30: 83-88.
- Ridder N de, Keulen H van (1990). Some aspects of the role of organic matter in sustainable intensified arable farming systems in the West-African semi-arid tropics (SAT). *Fertilizer Res.* 29: 299.
- Sas L, Rengel Z, Tang C (2001). Excess cation uptake, and extrusion of protons and organic acid anions by *Lupinus albus* under phosphorus deficiency. *Plant Sci.* 160: 1191-1198.
- Schroth G, Kolbe D, Balle P, Zech W (1995). Searching for criteria for the selection of efficient tree species for fallow improvement, with special reference to carbon and nitrogen. *Fertilizer Res.* 42: 297-314.
- Silwana T, Lucas EO (2002). The effect of planting combinations and weeding on the growth and yield of component crops of maize/bean and maize/pumpkin intercrops. *J. Agric. Sci.* 138: 193-200.
- Skovgård H, Päts P (1999). Reduction of stem borer damage by intercropping maize with cowpea. *Agric., Ecosyst. Environ.* 62:13-19.
- Staddon WJ, Duchesne LC, Trevors JT (1998). Acid phosphatase, alkaline phosphatase and arylsulfatase activities in soil from a jack pine (*Pinus banksiana* Lamb.) ecosystem after clear-cutting, prescribed burning and scarification. *Biol. Fertility of Soils* 27: 1-4.
- Stern WR (1993). Nitrogen fixation and transfer in intercrop systems. *Field Crops Res.* 34: 335-356.
- Tang C, Hinsinger P, Drevon JJ, Jaillard B (2001). Phosphorus deficiency impairs early nodule functioning and enhances proton release in roots of *Medicago truncatula* L. *Annals of Bot.* 88: 131-138.
- Tang C, McLay CDA, Barton L (1998). A comparison of proton excretion of twelve pasture legumes grown in nutrient solution. *Austr. J. Exp. Agric.* 37: 563-570.
- Tarafdar JC, Jungk A (1987). Phosphatase activity in the rhizosphere and its relation to the depletion of soil organic phosphorus. *Biol. Fertility of Soils* 3: 199-204.
- Tariah NM, Wahua TAT (1985). Effects of component populations on yields and land equivalent ratios of intercropped maize and cowpea. *Field Crops Res.* 12: 81-89.
- Uriyo AP, Mongi HO, Chowdhury MS, Singh BR, Semoka JMR (1979). *Introductory Soil Science*. Tanzania Publishing House, Dar es Salaam. 232pp.
- Vandermeer JH (1989). *The ecology of intercropping*. Cambridge: Cambridge University Press.
- Vanlauwe B, Diels J, Sanginga N, Merckx R (1997). Residue quality and decomposition: an unsteady relationship. In: Cadisch G, Giller K. (eds.) *Plant Litter Quality and Decomposition*. CAB International, Wallingford.
- Versaw WK, Harrison MJ (2002). A chloroplast phosphate transporter, PHT2;1, influences allocation of phosphate within the plant and phosphate-starvation responses. *Plant Cell* 14: 1751-1766.
- Vizzotto G, Pinton R, Bomben C, Cesco S, Varanini Z, Guglielmo C (1999). Iron reduction in iron stressed plant of *Acatinidia deliciosa* genotypes: involvement of PMFE (III) chelate reductase and H⁺ - ATPase activity. *J. Plant Nut.* 22: 479-488.
- Walker TS, Bais HP, Grotewold E, Vivanco JM (2003). Root exudation and rhizosphere biology. *Plant Physiol.* 132: 44-51.
- Watiki JM, Fukai S, Banda JA, Keating BA (1993). Radiation interception and growth of maize/cowpea intercrop as affected by maize plant density and cowpea cultivar. *Field Crops Res.* 35: 123-133.
- Willey RW (1979). Intercropping - its importance and research needs. Part I Competition and yield advantages. *Field Crops Abstracts* 32: 1-10.
- Willey RW, Osiru DSO (1972). Studies on mixtures of maize and beans (*Phaseolus vulgaris*) with particular reference to plant population. *J. Agric. Sci.* 79: 519-529.
- Willey RW (1990). Resource uses in intercropping systems. *Agric. Water Management* 17: 215-231.
- Wright AL, Reddy KR (2001). Phosphorus loading effects on extracellular enzyme activity in Everglades wetland soils. *Soil Sci. Soc. Am. J.* 65: 588-595.
- Yadav RS, Tarafdar JC (2001). Influence of organic and inorganic phosphorus supply on the maximum secretion of acid phosphatase by plants. *Biol. Fertility of Soils* 34: 140-143.
- Zhang F, Shen J, Li L, Liu X (2004). An overview of rhizosphere processes related with plant nutrition in major systems in China. *Plant and Soil* 260: 89-99.
- Zhang FS, Li L (2003). Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient-use efficiency. *Plant and Soil* 248: 305-312.
- Zhang FS, Li L, Sun JH (2003). Do interspecific interactions reduce

phosphorus fertilizer rates in the faba bean/maize intercropping *In* Proceedings of 2nd International Symposium on Phosphorus Dynamics in the Soil-Plant Continuum. 21-26 September 2003. Perth, Western Australia, pp 184-185.

Zang FS, Li L, Sun JH (2001). Contribution of above- and below-ground interactions to intercropping *In* Horst et al. (eds). Plant Nutrition – Food Security and Sustainability of Agro-ecosystems. Kluwer Academic Publishers, Dordrecht, pp 979–980.